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TEMPORAL AND VERTICAL VARIATIONS IN PHYTOPLANKTON COMMUNITY STRUCTURE AND ITS RELATION TO SOME MORPHOMETRIC PARAMETERS OF FOUR COLOMBIAN RESERVOIRS

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Abstract

Phytoplankton samples were taken at three depths within the photic zone of each of four reservoirs, Punchiná, Las Playas, El Peñol and San Lorenzo located in Antioquia department, Colombia. A total of 77 taxa were identified in the four reservoirs. Diatoms were not included. In all reservoirs, Chlorophyta was the dominant group. *Botryococcus braunii* was the dominant species at Punchiná, Las Playas and El Peñol reservoirs; *Cosmarium* sp. was the dominant at San Lorenzo. Temporal variation in phytoplankton showed two peaks of abundance, apparently related to precipitation. Taxonomic composition among samples from the same reservoir showed little variation. Community structure at different depths showed significant differences only at San Lorenzo reservoir. The inverse of β-diversity showed small values indicating high similarity among the reservoirs. Diversity showed no significant association with any morphometric factor evaluated (area, retention time, altitude and age).

Key Words: β-diversity, phytoplankton, reservoir limnology, tropical limnology

Resumen

Se efectuaron muestreos de fitoplancton en tres profundidades de la zona fótica de los embalses Punchiná, Las Playas, El Peñol y San Lorenzo, localizados en el departamento de Antioquia, Colombia. Se identificaron un total de 77 taxones en los cuatro embalses. Las diatomeas no fueron incluídas. En todos los casos las Cholorophyta fueron el grupo dominante. *Botryococcus braunii* fue el taxón de mayor densidad en los embalses Punchiná, Las Playas y El Peñol; y *Cosmarium* sp. en el embalse San Lorenzo. La comunidad fitoplanctónica mostró dos picos de abundancia aparentemente relacionados con la precipitación. En cada embalse, la composición de taxones entre muestreos varió poco. La estructura de la comunidad a diferentes profundidades mostró diferencias significativas únicamente en el embalse San Lorenzo. El inverso de la β-diversidad presentó valores bajos que muestran la alta similaridad entre embalses. La diversidad no mostró asociación significativa con ninguno de los parámetros morfométricos evaluados (área, tiempo de retención, altitud y edad).

Palabras clave: β-diversidad, fitoplancton, limnología de embalses, limnología tropical.

Introduction

The phytoplankton community is represented in every ecosystem by a group of specific forms whose variety, abundance and distribution are directly dependent on adaptation to changes in both biotic and abiotic characteristics of that ecosystem. Such a community develops into a complex assemblage of organic and inorganic particles and colloidal material which derives partly from terrestrial origins and partly from secretion, excretion and death of organisms in the water.

Mechanisms that cause replacements in time and space are of interest because phytoplankton resemble other organisms with respect to their requirements for growth and survival: only their need to remain in suspension is unique. As in any other community, species-specific differences in the balance of reproduction and mortality cause changes in species composition (Sommer 1989)

Diversity of this biocoenosis in tropical lacustrine ecosystems seems to be smaller than in temperate zone (Lewis 1978b). In relation to spatial heterogeneity the phytoplankton distribution results from the movement of the water mass, from the variability of the factors affecting growth and loss processes and, at a lower scale, from the degree of fluctuation or movement of the organisms that compose this community (Lewis 1978a).

The aims of this study are to describe the temporal and vertical variation patterns of the phytoplankton community within the photic zone of the Punchiná, Las Playas, San Lorenzo and El Peñol reservoirs, to examine the β-diversity of the phytoplankton community and the degree of similarity among the reservoirs and the relationships between diversity and reservoir area, age, altitude and retention time.

Materials and Methods

Study areas. The four reservoirs are part of the eastern Antioquian hydroelectric system that includes the Nare, Guatapé, Concepción, Bizcocho, San Carlos, Calderas and Tafetanes river basins, with a total area of 2239 km^2. The reservoirs are used for hydropower generation and are arranged in an interconnected line (Fig. 1). Table 1 shows their morphometric characteristics.

In the river basins, soil erosion and leaching are fast, the soil pH is low and limited by phosphorus (Espinal 1992). The climate of the area is the Cwb type in Köppen's international system, i.e. with wet and cooler winters and hot summers. During sampling time at each site in the four studied reservoirs, gradual decreases of water temperature were found inside the photic zone and they were considered sharpest in Las Playas reservoir. These conclusions are based on temperature profiles made only at 100% Io, 50% Io, 1% Io, half and bottom of the water column at the sampling point in each reservoir (Ramírez 1989).

In El Peñol reservoir a many studies have been carried out (Uribe & Roldán 1975, Björk & Gelin 1980, Orozco 1981, Roldán et al. 1984, Ramírez 1986a, 1986b, Sierra 1987, Vega et al.1990, 1992, Aguirre 1994, Mera 1994). Two papers have been published on the Punchiná reservoir (Horta 1985, Ramírez 1995). Routine unpublished studies have been carried out for the San Lorenzo and Las Playas reser-

Table 1. Principal characteristics of four studied reservoirs in Antioquia, Colombia.

Characteristic	Punchiná	Las Playas	San Lorenzo	El Peñol
Coordinates	6° 13' N, 74° 52' W	6° 29' N, 74° 58' W	6° 25' N, 74° 3' W	6° 10' N, 74° 10' W
Age (years in 1988)	9	8	7	22
Altitude (m)	775	980	1250	1887
Area (km^2)	3.6	7.5	10.6	62.5
Volume (Mm^3)	50	85	180	1169

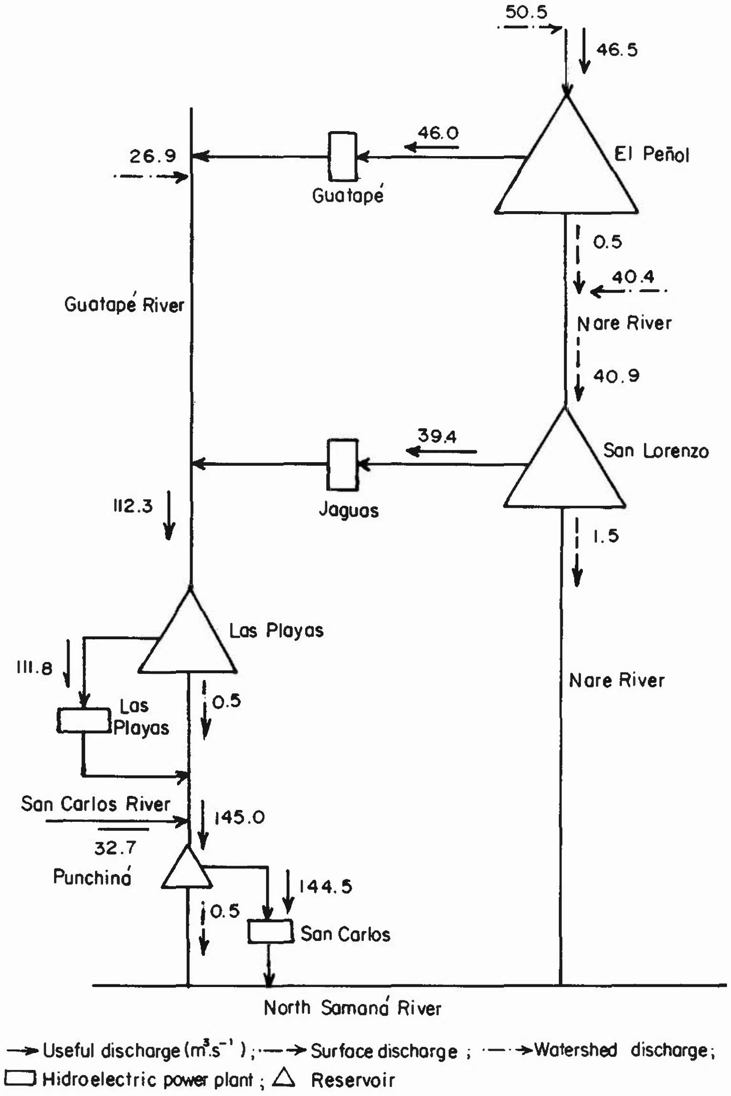

50.5
46.5
46.0
El Peñol
26.9
Guatapé
Guatapé River
0.5
40.4
Nare River
40.9
39.4
San Lorenzo
Jaguas
112.3
1.5
Las Playas
111.8
Las Playas
0.5
Nare River
San Carlos River
145.0
32.7
Punchiná
144.5
0.5
San Carlos
North Samaná River
Useful discharge (m^3.s^{-1}); Surface discharge; Watershed discharge;
Hidroelectric power plant; Reservoir

Figure 1. Part of the Nare-Guatapé hydroelectric system in Colombia, including the four reservoirs studied.

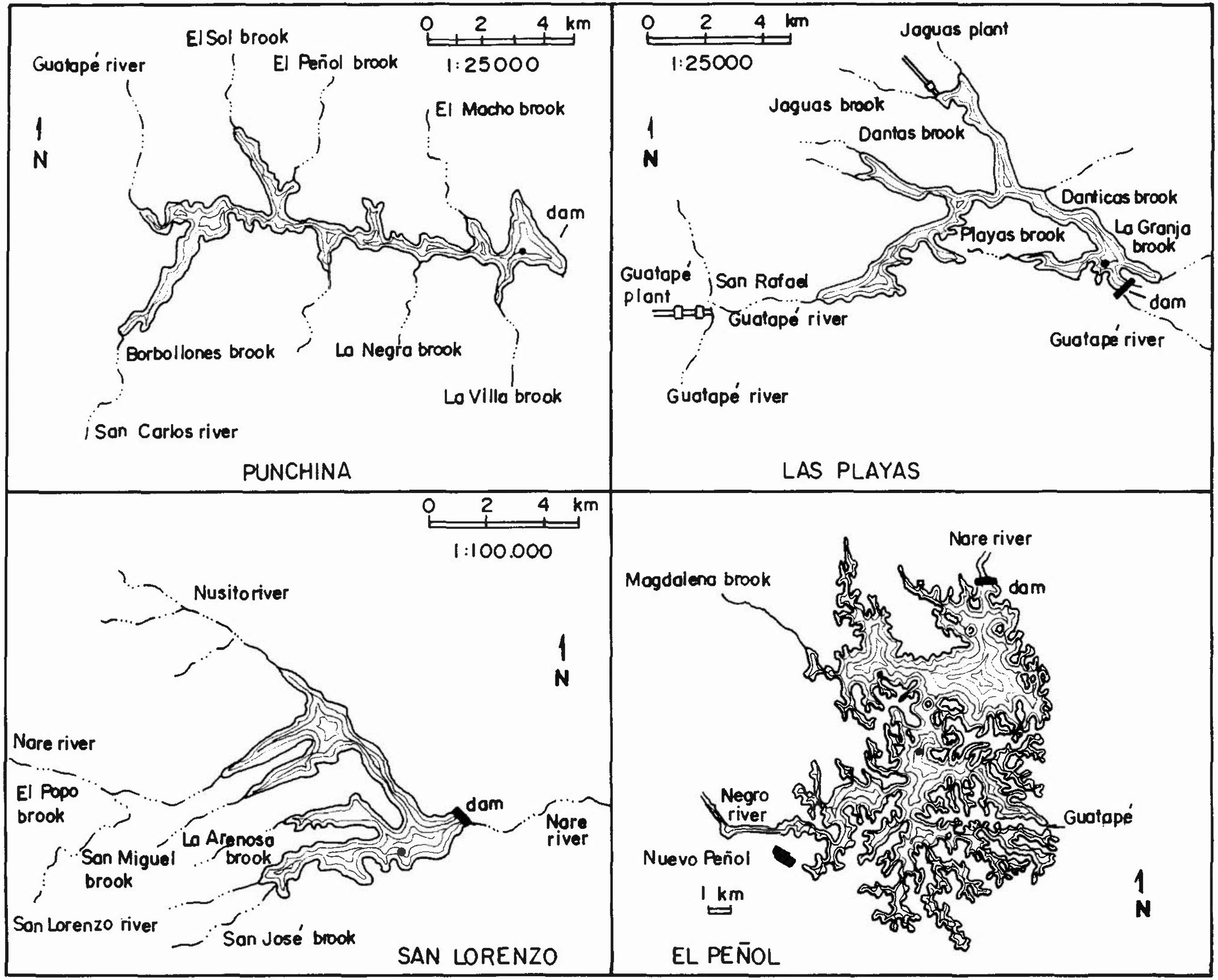

0 2 4 km
1:25000
Guatapé river
El Sol brook
El Peñol brook
El Macho brook
N
dam
Borbollones brook
La Negra brook
La Villa brook
San Carlos river
PUNCHINA
0 2 4 km
1:25000
Jaguas plant
Jaguas brook
Dantas brook
N
Danticas brook
La Granja brook
Playas brook
Guatapé plant
San Rafael
Guatapé river
dam
Guatapé river
Guatapé river
LAS PLAYAS
0 2 4 km
1:100.000
Nusito river
N
Nare river
El Popo brook
San Miguel brook
La Arenosa brook
dam
Nare river
San Lorenzo river
San José brook
SAN LORENZO
Nare river
Magdalena brook
dam
Negro river
Guatapé
Nuevo Peñol
1 km
N
EL PEÑOL

Figure 2. Location of the single sampling station in each of four reservoirs in Antioquia, Colombia.

voirs, by the Interconexión Eléctrica S.A. (ISA) and Empresas Públicas de Medellín (EPM-ESP).

SAMPLING AND DATA ANALYSIS. We took samples on six occasions (April, May, June, August, September and November 1988) at a single station located near the impoundment in Punchiná and Las Playas reservoirs, in a "tail" of the San Lorenzo reservoir and approximately at the center of El Peñol reservoir (Fig. 2). In every case, we took the samples with a Van Dorn bottle from the photic zone at depths corresponding to 100% Io, 50% Io and 1% Io. Attenuation depths of 50% Io and 1% Io correspond to 0.41 Zsd and 2.71 Zsd, respectively (Ramírez 1989).

We carried out counting following the Utermöhl method. A sample of 1 liter was taken and decanted in a funnel of the same volume for a period of five days. The sediment was collected in 30 ml flasks and completed to a volume of 100 ml. This volume was homogenized by shaking; a 10 ml aliquot equivalent to the volume of the sedimentation chamber was taken and phytoplankton were counted in 30 random fields at 400 x. According to McAlice (1971) 30 random fields detect 90-95% of the species present in a chamber bottom. The volume of the Utermöhl chamber, the magnification and the number of random fields were fixed in order to facilitate comparisons between reservoirs. We considered cells, cenobia, filaments and colonies as "individuals". We counted all organisms found except diatoms. We recorded the final results as individuals/l according to Ros (1979).

We estimated diversity, equitability and dominance according to Shannon & Weaver (1949), Pielou (1975) and Berger & Parker (1970), respectively. We estimated numerical species richness according to the number of taxa. To evaluate similarity among the four reservoirs, we used the inverse of Whittaker's (1972) β-diversity index (Umaña 1988). We measured the percentage of similarity between reservoirs through Morisita's (1959) formula, based on abundance data. We constructed the dendrogram by using UPGMA techniques (Crisci & Lopes 1983). We checked dependence and association of diversity with equitability and richness against Pearson's correlation index and simple linear regression. To associate diversity with age, altitude, area and retention time, we used also Pearson's correlation index, considering the case of several dates of dependent variables (6) for each independent one (reservoirs in this case). Statistical significance of the variation between depths and samplings for the biotic factors was obtained through a random blocks design. Three-way analysis of variance was used to test for significance among the four reservoirs. Significance of 95% of averages was computed by Tukey's test. All statistical analyses were performed through Statgraphics version 5.0.

Results

The phytoplankton of the four reservoirs includes 77 taxa (Table 2). We found 51 taxa in Las Playas, 48 in Punchiná, 46 in San Lorenzo and 39 in El Peñol.

The temporal variation of the total phytoplankton abundance and its relationship to precipitation showed the ocurrence of two abundance peaks (Fig. 3). This pattern is similar to those of dimictic lakes. We found a reduction in relative abundance of dominant species towards the lower limit of the photic zone. The relative abundance of taxa at different depths showed little variation at the four reservoirs, despite differences in light attenuation (Figs. 4-7).

We found no significant differences in equitability averages between depths in Punchiná (F = 0.693, p = 0.5256) and Las Playas (F = 1.03, p = 0.3902), as well as in diversity (Punchiná: F = 2.99, p = 0.096; Las Playas: F = 2.33, p = 0.1477) and dominance (Punchiná: F = 3.35, p = 0.0770; Las Playas: F = 2.92, p = 0.1003). For El Peñol reservoir, we found significant differences between depths in diversity (F = 4.36, p = 0.0434), equitability (F = 5.82, p = 0.0211) and dominance (F = 5.5, p = 0.0244) (Fig. 8A). For San Lorenzo reservoir, differences in diversity (F = 34.27, p = 0.0000), equitability (F = 32.56, p = 0.0000) and dominance

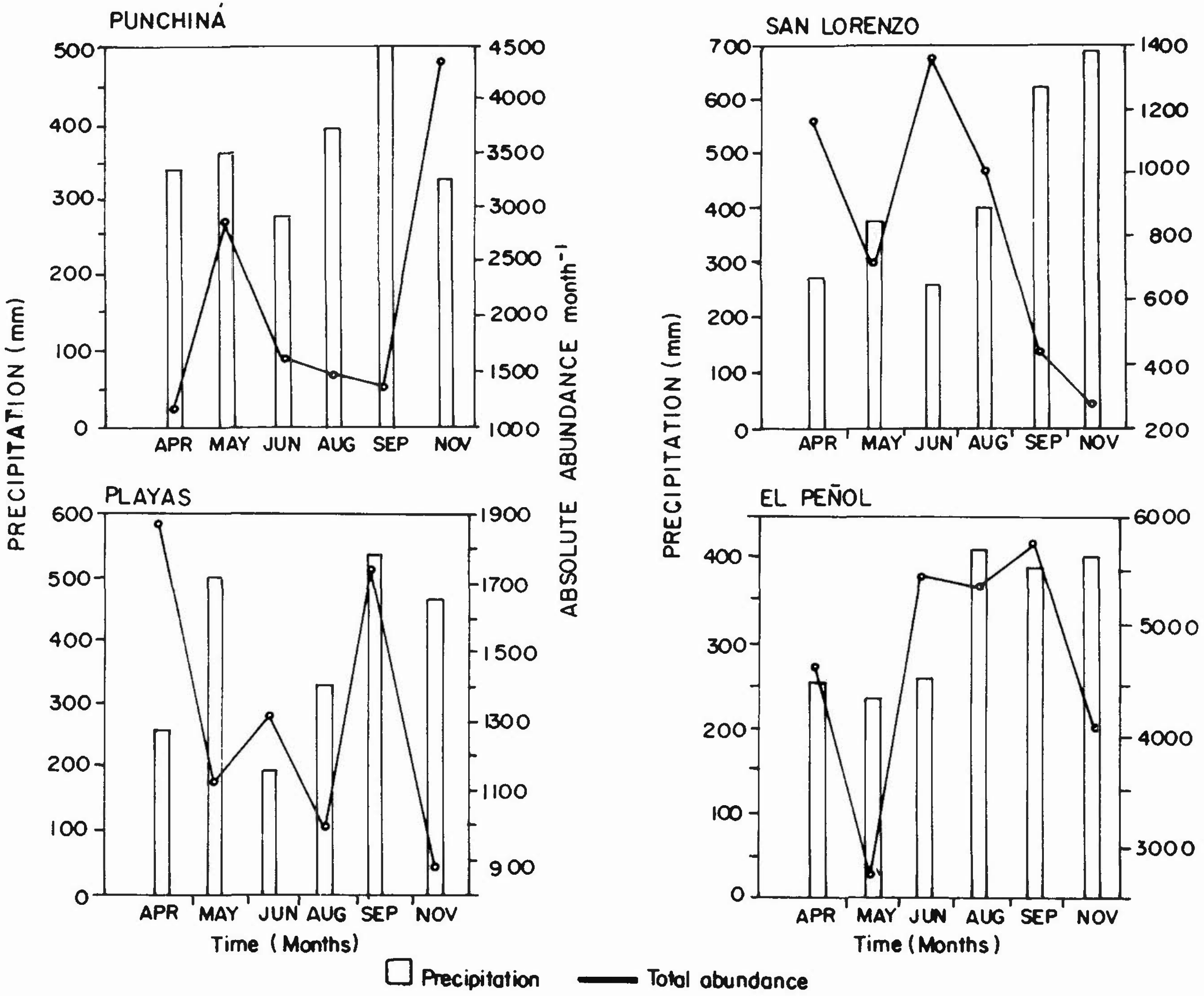


Figure 3. Temporal variations in total phytoplankton abundance and precipitation in four reservoirs in Antioquia, Colombia.

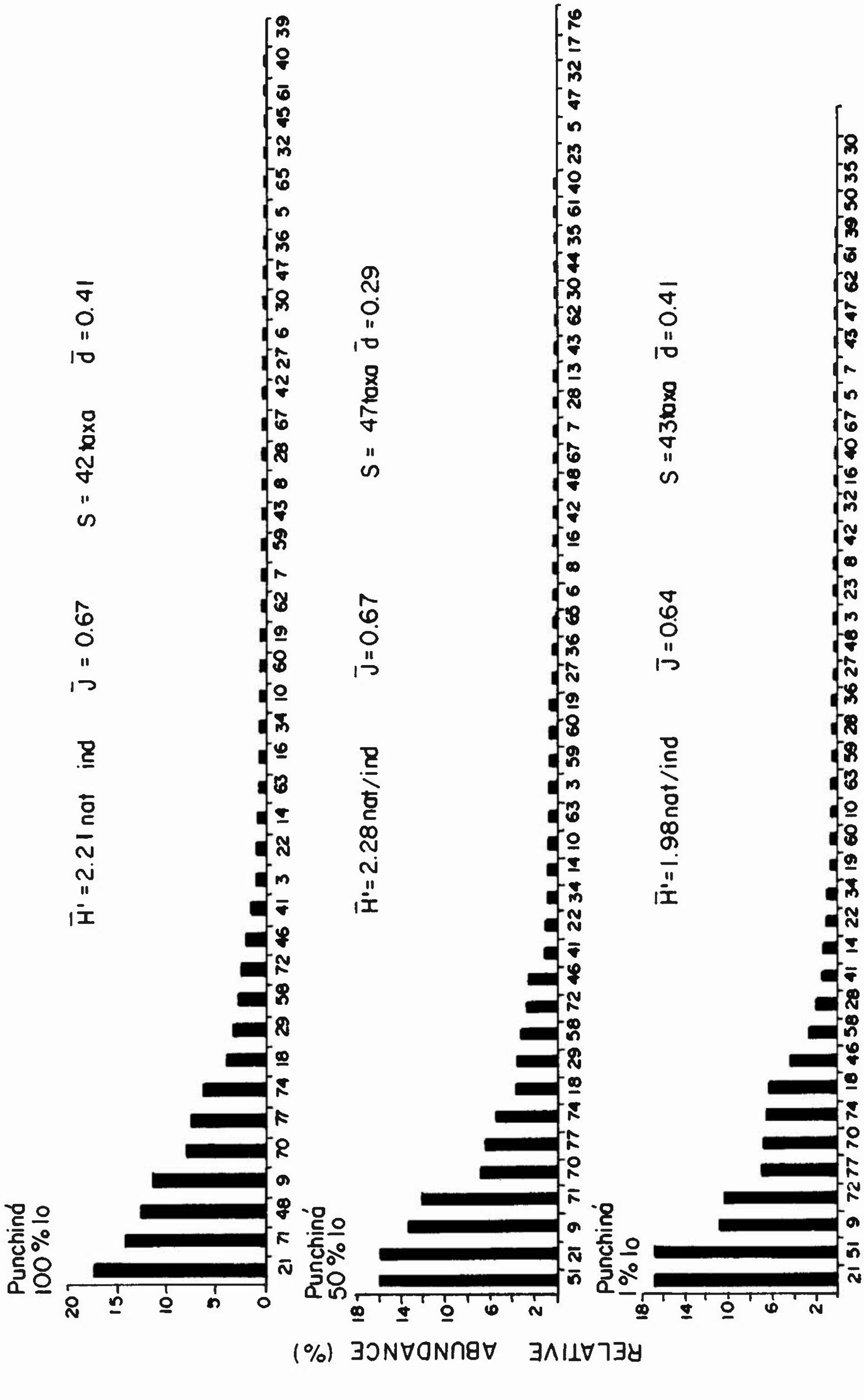


Figure 4. Importance curves in the photic zone of Punchiná reservoir, Colombia.

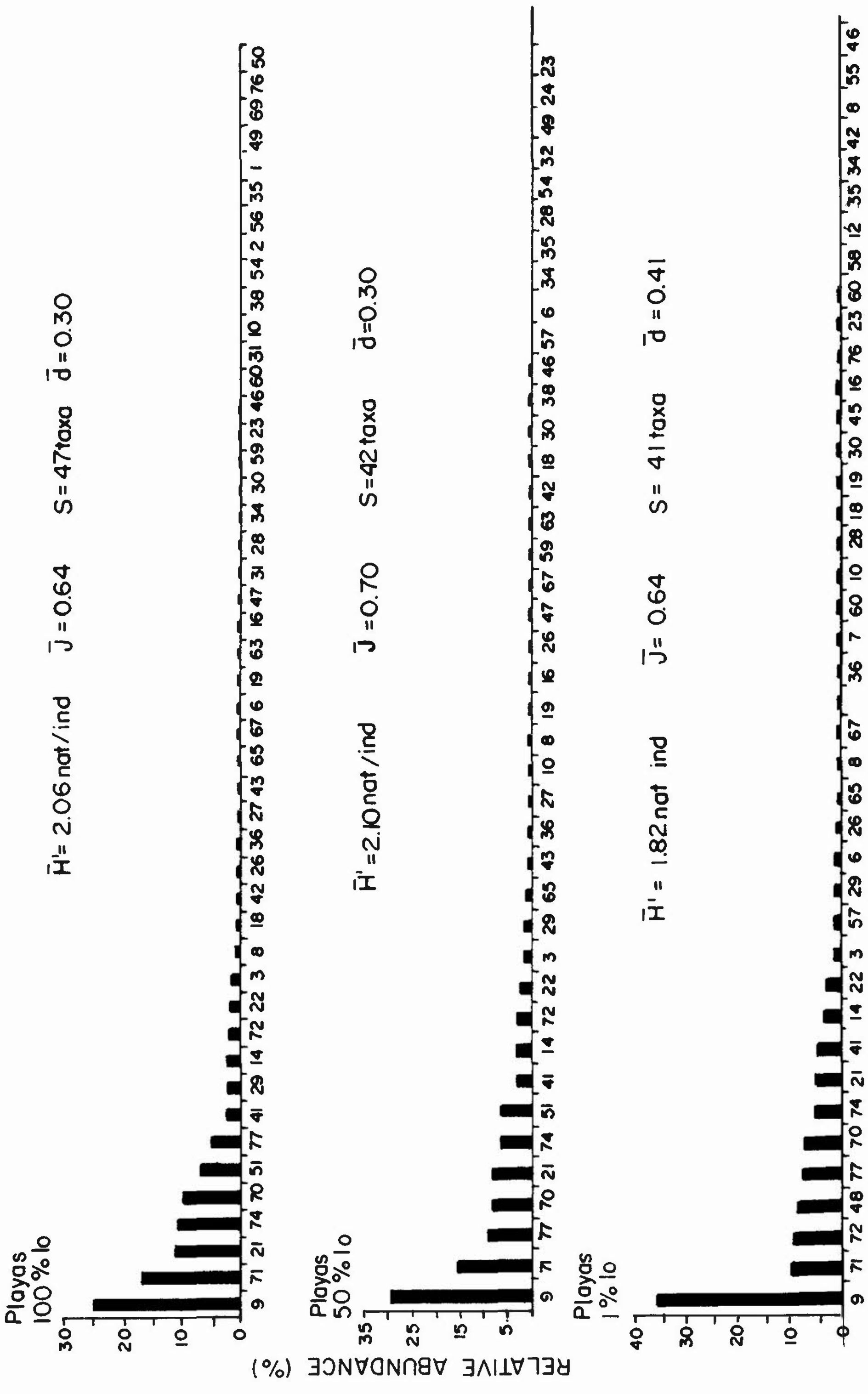


Figure 5. Importance curves in the photic zone of Las Playas reservoir, Colombia.

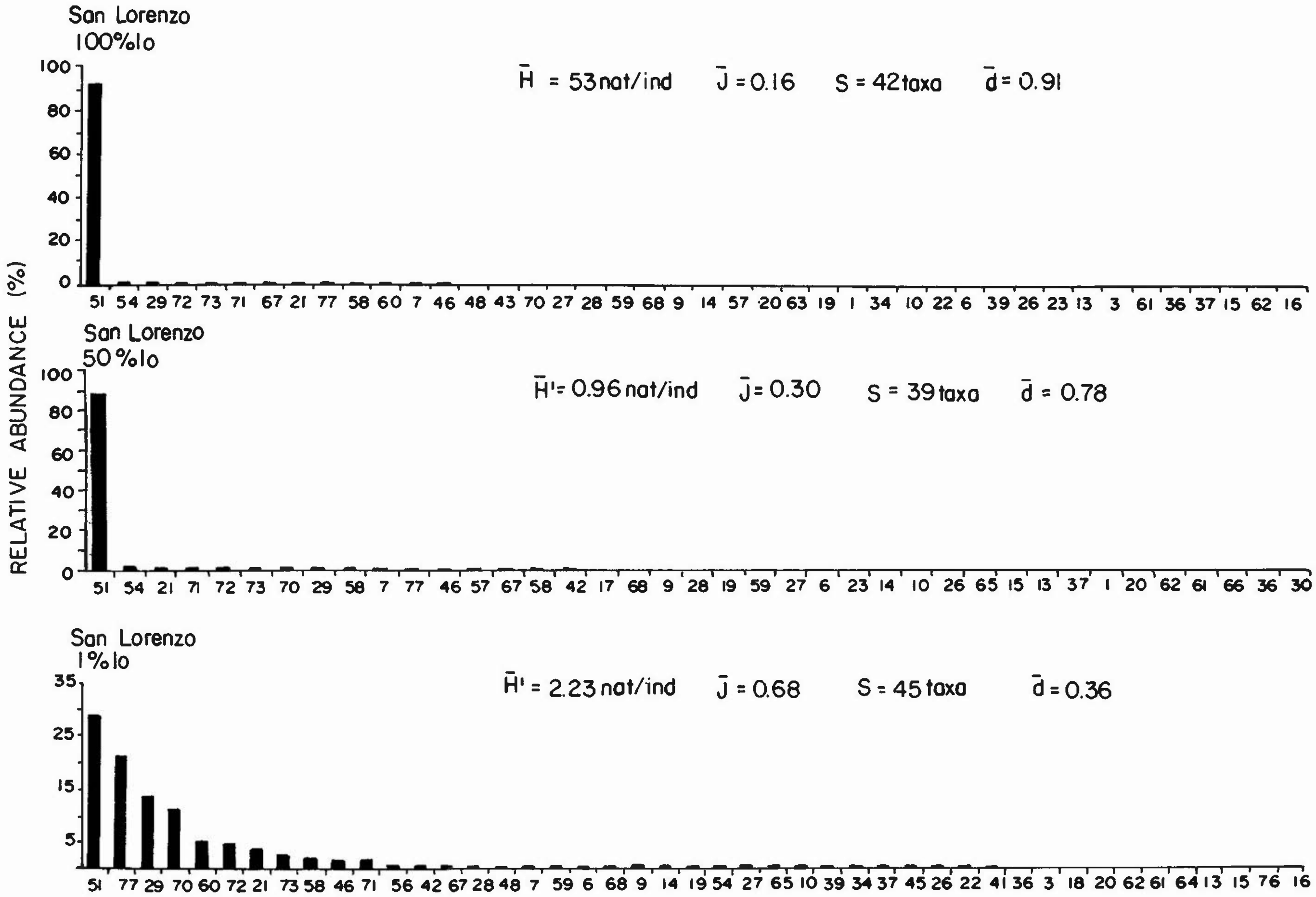


Figure 6. Importance curves in the photic zone of San Lorenzo reservoir, Colombia.

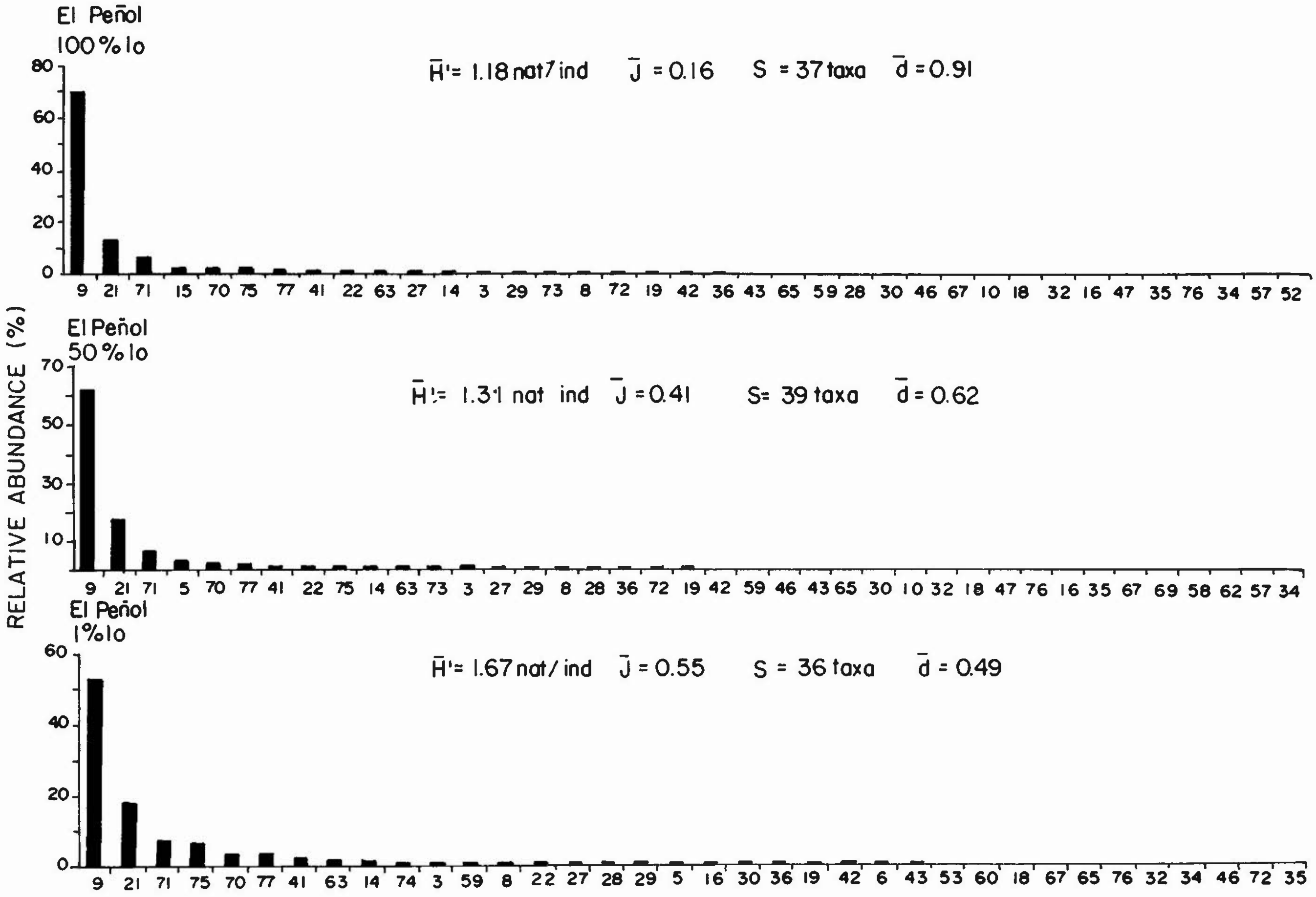


Figure 7. Importance curves in the photic zone of El Peñol reservoir, Colombia.

(F = 68.17, p = 0.0000) between different depths were highly significant. Using the Tukey test, averages of diversity, equitability and dominance measured at 1% of light attenuation, were different from those taken at 50% Io and 100% Io (Fig. 6 and 8B).

The Morisita index of similarity and the percentage of affinity between Punchiná and Las Playas were high, despite the considerable differences between their retention times. San Lorenzo presented low similarity (7.83%) to the other three reservoirs (Fig. 9). The β-diversity value was low (1.5). Diversity values were negatively correlated (r = - 0.80, p = 0.1659) with retention time, area and altitude but showed little correlation with the age of the reservoirs (r = 0.40, p = 0.4884).

Discussion

TAXONOMIC COMPOSITION AND ECOLOGICAL ASPECTS. The Class Nostocophyceae was represented by five species, but only *Chroococcus* sp. and *Oscillatoria* sp. ocurred in all four reservoirs. *Coelosphaerium kuetzingianum* was the most abundant at El Peñol, whereas *Borzia* sp. was the least abundant of the five taxa, occurring only in Las Playas. The relatively small densities of Nostocophyceae in the four reservoirs may be due to the shading produced by the dominant species in each. These develop special devices to float and to keep the species continuously within the photic zone. Thus, they get the optimum light intensity and limit its availability to other algal groups.

Representatives of the Dinophyceae are almost invariably found in the plankton of tropical lentic waters, but in very low abundance (Lewis & Riehl 1982). The water of the reservoirs contained two species of *Peridinium*, *P. gatunense* being dominant in both cases. *Peridinium* may present a capacity to concentrate C, N and P from the immediate environment, and thus organisms of this genus are able to survive and prosper in conditions of low external concentrations of such nutrients (Margalef 1983, Margalef et al. 1976). These conditions were probably largely prevalent in the reservoirs, particularly with respect to phosphorus (Ramírez 1989).

Dinobryon bavaricum, *D. sertularia* and *Phalansterium* sp. were the three identified Chrysophytes. The first species was present in all four sampling stations, whereas the second was found only at El Peñol. Since *Phalansterium* sp. usually occurs as attached (periphytic) colonies, its presence at El Peñol might be merely incidental. The Chrysophyceae are not dominant elements of tropical lacustrine phytoplankton, occurring sporadically and never in large populations (Lewis 1978b, Lewis & Riehl 1982). Furthermore, such organisms usually inhabit waters with relatively low nutrient concentrations (Margalef 1983). In many lacustrine ecosystems, there is also a positive correlation between ocurrence of *Dinobryon* and the decrease in orthophosphate during the rainy period (Lund 1965, Ramírez & Machado 1982, Dokulil & Skolaut 1991). Soluble reactive phosphorus was always found in very low concentrations in four reservoirs, but decreased considerably in the rainy season (Ramírez 1989). The abundance of the *Dinobryon* species has been interpreted as competitive dominance under conditions of phosphorus limitation (Sandgren 1988, Dokulil & Skolaut 1991). The latter authors have suggested that iron is an important limiting microelement for *Dinobryon*. However, iron concentrations in all sampling sites were high and increased from surface to the bottom waters (Ramírez 1989).

Cryptomonas sp. was the only taxon of the Cryptophyceae to occur in all four reservoirs. Members of this group are almost universally present in tropical lentic waters, but rarely in high abundance (Lewis & Riehl 1982). *Cryptomonas* is considered one of the most ubiquitous in soft waters (Lewis & Weibezhan 1976, Lewis 1978b, 1978c), as it was in the present case.

Euglenophyceae was represented by two species of *Trachelomonas* and one each of *Euglena* and *Phacus*. *T. volvocinopsis* and *Euglena* sp. were the most abundant of all euglenophytes present in all four reservoirs. Euglenophyceae were never very numerous, and their abundance presents low variation. They play a minor role in tropical lacustrine ecosystems, though several species of *Trachelomonas* are usually found (Lewis 1978b). In general, Euglenophyceae are abundant in waters rich in organic matter (Margalef 1983, Esteves 1988); this was not the prevailing situation at the four reservoirs. The development of *Trachelomonas* in the phytoplankton community is usually related to adequate concentrations of ammonium (Wetzel 1983), a characteristic not prevalent in all sampling stations (Ramírez 1989).

Differences in taxonomic composition between the algal floras of natural lakes and reservoirs are almost nonexistent. Such a taxonomic composition is thus a widespread event with a pantropical character (Lewis 1978b). Chlorophytes are the most diversified group of organisms in the plankton of tropical lentic environments with moderate to low salinity. Usually, this group accounts for almost 50% of the total taxa identified in tropical environments. Chlorophyta (Chlorophyceae, Oedogoniophyceae and Zygnemaphyceae) presented the greatest relative abundance in all four sampling stations, especially in San Lorenzo and El Peñol. Chlorococcales and Zygnematales were the dominant orders of chlorophytes in all four sampling stations. Regarding the Chlorococcales species, *Botryococcus braunii* was the prevalent at Las Playas (28.4% of the total) and El Peñol (64.1% of the total). At Punchiná, this species was codominant (12%) together with *Elakatothrix viridis* (16.5%), *Cosmarium* sp. (14.8%) and *P. gatunense* (14.8%). *Botryococcus* is a euplankter, very well represented in most Colombian reservoirs. It is common in nutrient-rich waters, and produces "water blooms" at various times of the year (Márquez & Guillot 1987). Notwithstanding, Wetzel (1983) considered *B. braunii* as typical of oligotrophic, neutral to slightly alkaline, nutrient poor waters, while Margalef (1983) considered the same species as characteristic of mesotrophic to eutrophic lakes with poorly mineralized waters. This seems to be the case in all of our sampling sites. However, Hutchinson (1967) noted that *Botryococcus* can be extremely abundant in different systems where conditions are highly variable.

Cosmarium sp. (83.5%) is highly dominant at San Lorenzo. Although this taxon seems to depend exclusively on carbonic acid, in San Lorenzo the genus frequently developed in the "tails", where it can tolerate and use the organic matter brought in by tributaries (Márquez & Guillot 1987).

A water body is in its stable phase when a few algal species contribute more than 80% of its total biomass and when such species remain dominant for a period longer than two weeks (Padisák et al. 1993). In San Lorenzo, *Cosmarium* sp. represented 83.5% of the total abundance; in El Peñol, the three dominant species together contributed 84.9% of total abundance. The communities present at the sampling station appear to be fairly close to stability, a condition perhaps related to retention time. The retention time in these reservoirs (Peñol= 280 days, San Lorenzo = 59 days), can be considered as a small-scale disturbance that leads to the occurrence of competitive exclusion and a decrease in diversity (Figs. 6 and 7). For Punchiná and Las Playas (Figs. 4 and 5), where retention times were much shorter (6 and 9 days, respectively), the joint contribution of the four dominant species amounted to 54.7% in the former and 60.2% in the latter. These two ecosystems probably do not attain an advanced succesional phase, since they are subjected to disturbances of intermediate intensity (1 to 9 days), especially represented by the short retention times. This type of disturbance allows a regression to the initial phases of succession, when species diversity is higher (Connel 1978, Padisák et al. 1993).

TEMPORAL VARIATION. Phytoplankton community showed two abundance peaks during high precipitation at the Punchiná and Las Playas, whereas at San Lorenzo and El Peñol at least one peak was observed in the dry season (Fig. 3). As a consequence, high values in the coefficient of variation were found in each reservoir (Punchiná: 39.5%, Playas: 31.8%, San Lorenzo: 51.9%, Peñol: 25.5%). These patterns resemble those of dimictic lakes.

Like other tropical lakes, the four reservoirs presented dense phytoplankton populations throughout the year, and a low variation in their species compositions. As a consequence, species diversity decreased when equitability was affected. Table 3 indicates that diversity in all sampling stations showed a positive and highly significant dependence upon equitability. So, even if some species are lost by disturbance in each reservoir, the remaining species maintain the diversity.

Periods of maximum and minimum abundance were not determined by nutrient concentration, as suggested by Talling (1966), since all sampling sites presented low nutrient concentrations (except for ammonium) year-round (Ramírez 1989). The only significant correlation between phytoplankton density and nutrients (nitrate in this case) was found in San Lorenzo ($r = 0.70$, $p = 0.00128$).

The cause for alternation of maximum and minimum periods on phytoplankton density might be the well-marked succession of wet and dry seasons and their influence on radiation availability (Lewis 1978b, Zafar 1986). The increases in vertical mixing and turbulence caused by precipitation, wind and physical forces in each reservoir may lead to very strict environmentally-caused selective pressures on the associated species, and thus influence their survival and reproductive strategies (Tundisi 1990). Mixing and turbulence patterns prevent nutrient depletion and allow dominance of some species. All four sampling sites correspond to type A in Melack's (1979) classification system, with pronounced seasonal fluctuations in phytoplankton abundance with coefficents of variation greater than 25%. These fluctuations are caused by oscillations of wind-induced vertical mixing, increased river discharge, rainfall, and associated changes such as measured turbidity, nutrients and flushing rate. Most tropical lakes exhibit this pattern. In contrast, type B lakes show very low coefficients of variation for phytoplankton abundance and photosynthetic rates (25.0%) and little coupling of their fluctuations to the seasonality of the weather (Melack 1979).

VERTICAL VARIATION. Reduction of phytoplankton abundance towards the limit of the photic zone is well documented, and frequently related to the hostile effect of the short-wave area of the light spectrum and to the limiting character of the water surface, below which cells are lost to the bottom but never replenished from above (Margalef et al. 1976). Reduction is also caused by the imbalance between growth and dispersion rates due to turbulence, since dispersion rates tend to be greater in the photic zone. Vertical variations in reservoirs are also coupled with vertical variation patterns for temperature, dissolved oxygen, nitrates, orthophosphates and light intensity (Tundisi 1990).

The slight variation of equitability, diversity and dominance with depth at Punchiná and Las Playas (Figs. 4 and 5) is explained because the mechanical influence of wind in the photic zone in these two reservoirs suspends the phytoplankton taxa. Low retention time patterns of reservoirs can be another explanation, since low retentions are significatively altered by horizontal flow that breaks the water column.

Differences between depths for diversity, equitability and dominance were significant in El Peñol because the dominant species (*B. braunii*) diminished its relative density to the limit of the photic zone (1% Io, Fig. 7). Tukey's test showed that for these three variables only depth corresponding to 100% Io and 1% Io of vertical light attenuation showed significant differences (Fig. 8A).

Highly significant differences in diversity, equitability and dominance between depths at San Lorenzo (Figs. 6 and 8B) ocurred due to low wind action in the sampling station. As a consequence, the formation of sharp thermal gradients was observed and the speed of phytoplankton sedimentation was reduced. An increase of density is produced in the photic zone, where conditions of

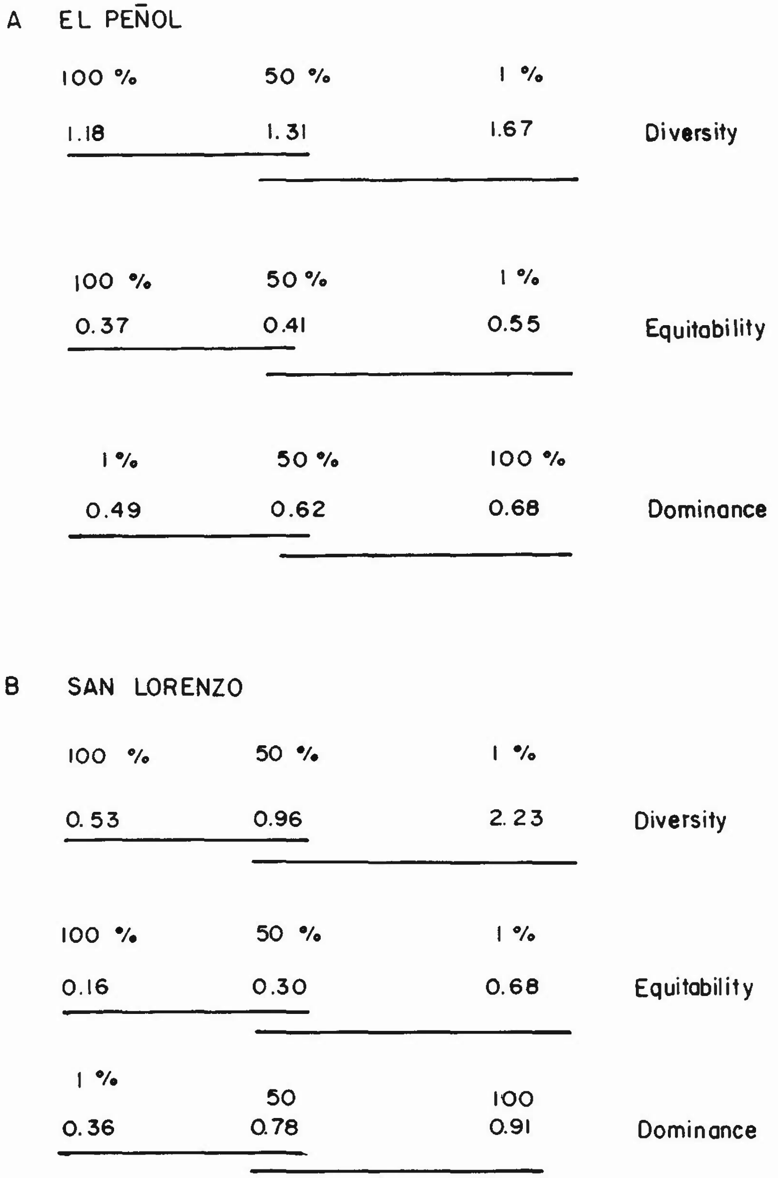
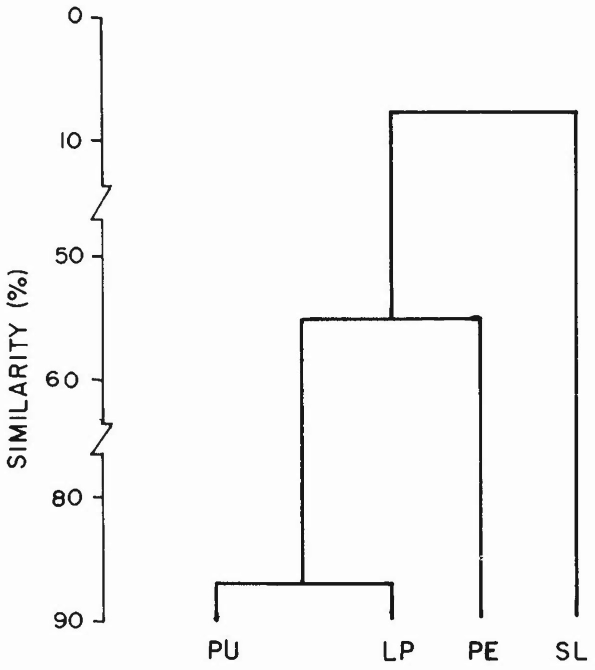


Figure 8. Mean comparisons for diversity, equitability and dominance for El Peñol (A) and San Lorenzo (B) reservoirs, Colombia.



	Punchiná	Las Playas	San Lorenzo	El Peñol
Punchiná (PU)		80.71	6.03	40.28
Las Playas (LP)		-	15.36	70.29
San Lorenzo (SL)			-	2.10
El Peñol (PE)				-

Figure 9. Cluster analysis for total phytoplankton abundance at four Colombian reservoirs, based on Morisita's similarity index.

light, nutrients and protection against grazing could be temporarily advantageous.

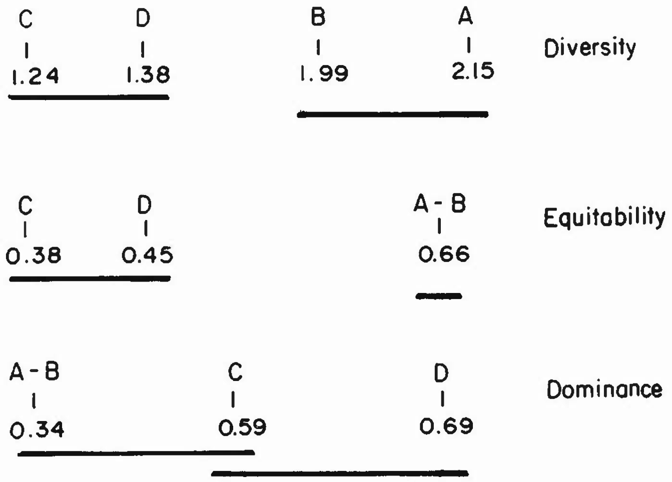
SIMILARITY BETWEEN RESERVOIRS. The dominant taxa at Punchiná are almost the same as those found at Las Playas, despite their greater abundance values at the former (Figs. 4 and 5). As a consequnce, similarity between these two reservoirs was high (80.71%, Fig. 9). The short retention time of both reservoirs allows the establishment of a well-defined phytoplankton community. Other factors which might influence similarity between these two reservoirs are the altitude and the water outlet from Las Playas into Punchiná after a relatively short course through the Guatapé river (Fig. 1). Consequently, similar values for diversity, equitability and dominance between Punchiná and Las Playas are to be expected (Fig. 10).

The high values of affinity between Las Playas and El Peñol (70.29%, Fig. 9), despite the considerable differences between their retention times, are probably due to the fact that Las Playas receives the water from El Peñol (Fig. 1). Despite the difference in altitude, the organisms that reach the second reservoir would be highly capable of adaptation to the new environment, since the physical and chemical composition of the water of two reservoirs is very similar (Ramírez 1989).

San Lorenzo presented low similarity values (7.83%, Fig. 9) in relation to the other three reservoirs, most probably because 1) it was practically isolated from the rest of the hydrographic system during the sampling time; 2) because sampling place is located at a "tail" in the reservoir; and 3) because the dominant taxon (*Cosmarium* sp.) is distinct from those of the other reservoirs (Fig. 6).

Lewis (1978b) predicted that among tropical lakes of same geographic region, there will be considerable difference in species composition (a high β-diversity). The low β-diversity in Table 4 clearly indicates that the changes in species composition in the four reservoirs were of small magnitude, since the water bodies are interconnected and show great similarities. This is confirmed by the value of the inverse of β-diversity, which clearly shows that their degree of conjunct similarity (66.4%) is high.

RELATIONSHIP TO ALTITUDE, AGE, AREA AND RETENTION TIME. No significant dependence between diversity and morphometric variables was detected, probably because the sampling frequency was low (n = 6). Despite this fact, the retention time and flow rate are factors which affect phytoplankton growth. Significant increase in abundance of these organisms occurs after two or three weeks (Henry et al. 1985). In ecosystems with comparatively short retention, the phytoplankton species with high reproductive rates (r-strategists in Margalef 's sense, C-strategists in Reynolds' sense)



A: Punchiná B: Las Playas C: San Lorenzo D: El Peñol

Figure 10. Mean comparisons for diversity, equitability and dominance among four Colombian reservoirs.

can replenish the losses in biomass caused by removal of organisms via the fast flow rate through the sluice way. Such removal might be considered an "intermediate disturbance" which represents a dominant selective pressure during determination of the phytoplankton species composition in the water body. When retention time is low, phytoplanktonic organisms are composed of nannoplankton (50 m, after Dickman 1969) and/or picoplankton (2-0.2m, after Tundisi 1990). An increase in diversity and a consequent decrease in competition is produced and can delay the exclusion process. In water bodies with low retention time, species composition falls into the first maturity stages of a succesional series (Margalef et al. 1976). Organisms that reproduce at a low rate probably will be removed from the reservoir before reaching a significant biomass. As the retention time increases, the species represented by larger-sized organisms (k-strategists in the Margalef sense, S-strategists in Reynolds' sense) reach higher abundance and biomass, though the diversity of the phytoplankton community is reduced.

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